Post-fire and post-salvage regeneration dynamics of *Picea mariana* (black spruce) and *Pinus banksiana* (jack pine)

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ABSTRACT

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The chapters in this thesis examine the post-fire and post-salvage natural regeneration dynamics of *Picea mariana* (black spruce) and *Pinus banksiana* (jack pine). The first examines the compaction of the post-fire organic layer by snow and its effects on seedling recruitment. We found that compression occured but at an insufficient rate to seriously increase seedling establishment. There was a positive relationship between the initial thickness of the burned organic layer depth and the subsequent amount of compression. The second chapter examines the post-fire abscission schedule of these two species. We found that seed abscission begins immediately following fire, with jack pine having a faster rate of abscission than black spruce. The third chapter presents a post-fire and post-salvage natural regeneration model that includes (1) the abscission schedule from Chapter two, (2) seed availability as a function of basal area, salvage proportion and timing; (3) seedling survivorship as a function of seed mass, seedbed type frequencies, first summer ash, and granivory; (4) seedling and seed mortality as a function of salvage operations; and (5) re-dispersal of salvaged seeds via a chipper. Simulations indicate that a delay in salvage timing and/or a reduction in salvage proportion can yield adequate natural regeneration densities, thereby foregoing the costly need to plant.

Contributions of Authors

The three chapters within this thesis were co-authored by the following authors: T.B. Splawinski, D.F. Greene, S. Gauthier, and Y. Bergeron. I was first author and responsible for developing the research design and questions, obtaining the required data, analyzing the results, and writing each of the three chapters. The remaining authors contributions were strictly editorial in nature.

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Introduction

Fire is the dominant disturbance in the boreal forest of North America (Johnson 1992; Payette 1992) and thus is the primary control on forest community structure and composition. Over the last few centuries, the return time for wildfires ranged from 50 to 150 years (Johnstone *et al.* 2004); however, the frequency and intensity of wildfires in the Canadian boreal forest has certainly increased over the last few decades (Lindenmayer. 2006), and is now responsible for burning an average of 2.8 million ha/yr (Shetler *et al.* 2008). The great majority of area burned is due to large (>200 ha), high intensity, stand-replacing crown fires (De Groot *et al.* 2004; Shetler *et al.* 2008) that typically lead to the initial dominance of species adapted to this disturbance regime via aerial seedbanks or reliable asexual recruitment. It is only the landscape-scale variation in fire frequency and intensity that has yielded a heterogeneous distribution of forest stands of differing age-classes and composition (Schmiegelow *et al.* 2006; Morissette *et al.* 2002).

Black spruce (*Picea mariana*) and jack pine (*Pinus banksiana*) are the most common tree species in the boreal forest (Charron and Greene 2002; De Groot *et al.* 2004; Greene *et al.* 2006). Their ability to rapidly colonize burned areas and outcompete other vegetation has led to their dominance in regions characterized by a short fire return interval. Spatially the distribution of black spruce and jack pine is not uniform; black spruce is usually found in wet, nutrient-poor sites dominated by thick layers of *Sphagnum* moss while jack pine is found on drier but also nutrient-poor sites (Miyanishi 2001; Miyanishi and Johnson 2002) dominated by thin layers of feathermoss or lichens (Shetler *et al.* 2008). Their distribution is therefore determined by local topography: black spruce dominates low-lying areas while jack pine dominates hills and ridge-tops (Miyanishi

2001; Miyanishi and Johnson 2002). Organic layers in black spruce stands are deeper than those found in jack pine stands due to higher water content and decreased rates of decomposition. As an example Shetler *et al.* (2008) observed that organic matter in sites dominated by *Sphagnum* moss (wetter sites) was more than twice of that of dryer sites dominated by feather moss and/or lichens. Greene *et al.* (2007) observed that sites wet sites dominated by *Sphagnum* can have organic layers as thick as 31 cm.

Black spruce and jack pine quickly re-establish after large fires through the use of aerial seedbanks (Charron and Greene 2002; Greene *et al.* 1999; Greene and Johnson 1999; Greene *et al.* 2006). These species are considered serotinous; i.e. they maintain more than one cohort of seeds on their branches (Greene and Johnson 1999; Enright *et al.* 1998; Lamont *et al.* 1991; Gauthier *et al.* 1993). The heat from the passing flaming front opens these cones, thus allowing the seeds to abscise (Greene *et al.* 2006) while smoldering combustion reduces the organic layer on the forest floor (Miyanishi and Johnson 2002). Some old cones will eventually open in the absence of fire, but any seeds abscised before the fire will be killed by the smoldering combustion (Miyanishi 2001).

The availability of suitable seedbeds (Dyrness and Norum 1983; Greene *et al.* 2007; Miyanishi 2001; Miyanishi and Johnson 2002), seed sources (Johnstone *et al.* 2004; Zasada *et al.* 1992) and weather (De Groot *et al.* 2004) are crucial in determining post-fire conifer regeneration

Seedbeds

Boreal forest trees produce small seeds with a minimal investment of maternal resources; in turn these small germinants are prone to desiccation (Greene *et al.* 2006; Greene *et al.* 2005; Greene *et al.* 1999). Greene *et al.* (2006) found that seed mass of

boreal tree species ranged from 0.5 mg for aspen (*Populus tremuloides*) up to 7 mg for fir (*Abies balsamea*), while germinant length ranged from 0.5 to 3 cm for these same two extremes. It is therefore not surprising that organic layer thickness has been identified as crucial in determining recruitment of small-seeded aerially dispersed species (Greene *et al.* 2006; Greene *et al.* 2005; Greene *et al.* 1999). Thick organic layers are porous, and therefore have poor water retention (Greene *et al.* 2005; Greene *et al.* 1999) resulting in increased, if not total germinant mortality. The only exception to the lethality of organic seedbeds is where (1) the layer is so thin that the radical of even a small germinant can quickly penetrate to the underlying (much lower porosity) humus; and (2) the organic layer is composed of *Sphagnum* that remains wet throughout the summer. Occasionally, feathermosses with a nearby watertable can also remain quite wet and thus serve as a good seedbed. Seedbeds that engender the highest rates of germination and survivorship are those that are able to retain moisture for prolonged periods, especially during periods of drought (Calogeropoulos *et al.* 2004), and provide a suitable rooting medium (Greene *et al.* 2007). Suitable seedbeds include exposed mineral soil (Kemball *et al.* 2006), thin humus (De Groot *et al.* 2004; Greene and Johnson 1999), rotting wood (Greene *et al.* 1999), *Polytrichum* (Charron and Greene 2002), and *Sphagnum* (Greene *et al.* 2004; Calogeropoulos *et al.* 2004). Unsuitable seedbeds include charred wood, solid wood, a thick non-sphagnum organic layer, burnt organics, thick leaf litter, feathermosses, lichen, and other substrates that dry quickly (Charron and Greene 2002; De Groot *et al.* 2004; Greene and Johnson 1999; Greene *et al.* 2004).

Fire and burn severity influences species regeneration and stand composition by reducing organic layers to burnt duff of varied post-fire thickness (Greene *et al.* 2005;

Johnstone and Chapin 2006; Dyrness and Norum 1983; Miyanishi 2001; Miyanishi and Johnson 2002) thereby creating a large variation in potential seedbeds (Charron and Greene 2002; Johnstone and Chapin 2006). Post-fire seedbeds typically consist of 30% - 90% burnt duff composed of thin charred organics and thick charred mosses and litter, 10% - 30% exposed mineral soil and humus, and surviving *Sphagnum* (Greene and Johnson 1999). While Greene *et al.* (2006) found that smoldering combustion leads to on average 40% cover of very thin organic layers, they showed that this number varied tremendously from one fire to the next, and that thin organic layers were rare in lowland sites.

In intact stands within the boreal forest, thin organic layers are very rare (Greene *et al.* 2006), especially in low-lying black spruce sites, which tend to have deep organic seedbeds. Indeed these stands are generally characterized by thick moss or leaf litter layers unfavorable for establishment (Lepage *et al.* 2000). Greene *et al.* (2006) observed that 5 to 15 cm depths are common in intact stands which is much too thick for germination and survivorship of small seeded species. Perhaps the only suitable seedbed found in intact stands are rotten logs (falling leaves are re-entrained by wind); however, they account for only 1-5% of the forest floor (Greene *et. al.* 2006). Post-fire seedbeds created by smoldering combustion are therefore better for regeneration because moss and litter layers are reduced (Greene *et al.* 2006), allelopathic substances are destroyed, light availability and soil temperatures increase, and competitors, granivores, herbivores and pathogens are reduced or removed (Lamont *et al.* 1991).

The thickness of the organic layer is dependent on rates of input and decomposition, which are influenced by temperature, moisture, hydrology and litter

characteristics (Miyanishi 2001; Miyanishi and Johnson 2002). The amount of organic material consumed by smoldering combustion is dependant on pre-fire depth (Dyrness and Norum 1983), density (Miyanishi and Johnson 2002), and moisture content of the organic layer (Dyrness and Norum 1983; Greene *et al.* 2007; Shetler *et. al.* 2008). Thick organic layers with high moisture content, e.g. *Sphagnum*, will have less combustion than those that are dry (Shetler *et al.* 2008). On average, there is approximately a 50% reduction in organic layer depth due to smoldering combustion (Greene *et al.* 2007; Shetler *et al.* 2008). Greene *et al.* (2007) found that mean organic depth in burned *Pinus banksiana* and *Picea mariana* stands in Northern Quebec was 13 cm; by contrast, in a poorly drained intact stand dominated by sphagnum the mean depth was 31 cm. Similar results were obtained by Dyrness and Norum (1983), who found a mean organic layer reduction of 45%; i.e. almost half the pre-fire organic layer.

Tree recruitment occurs typically within the first six years following fire (Miyanishi and Johnson 2002; Johnstone *et al.* 2004). Due to rapidly drying seedbeds (Greene *et al.* 1999) and the negative effects of ash (De Groot *et al.* 2004; Thomas and Wein 1985) age-specific survivorship is often lowest in the first year following fire (Greene and Johnson 1999). Subsequently, it increases as the ash is leached away. Where angiosperm competitors are dense and have rapid growth (i.e. where shrubs and trees are asexually recruiting) the age-specific survivorship begins to decline a few years after the fire as litter builds up on the previously good seedbeds.

For aerial seedbank species most cohorts occur within the first few years post-fire not merely because of the clemency of the seedbeds but also because of the rapid abscission of the stored seeds (Greene *et al.* 2004; De Groot et al, 2004; Johnstone et al,

2004; Calogeropoulos et al, 2004). The limiting role of the seedbed clemency is best shown for non-aerial seedbank species such as white spruce where the strongest pulse of recruitment occurs when there is a mast crop within three years of a fire (Peters *et al.* 2005).

Salvage

Prior to about 1990 burned forests were mostly ignored, but subsequently salvage has been increasingly used in Canada as each province has reached its annual allowable cut and thus cannot forego the loss of wood volume due to fire or pests (Greene et al, 2006). Salvage is predicted to increase globally because of road construction, increased fire frequency and increased demand for timber products (Lindenmayer 2006; Lindenmayer and Noss 2006; Morissette *et al.* 2002).

An additional reason for salvage is perhaps the public's negative perception of fire as both wasteful and unnatural (Schmiegelow *et al.* 2006). The misguided view that burned areas have little value to plants and animals (Morissette *et al.* 2002), the belief that these disturbed areas will attract insects that may damage adjacent stands, and that burned trees will provide additional fuel for future fires, have also been used to justify salvage (Lindenmayer and Noss 2006). Wildfire has long been perceived as a catastrophic event by both the public and scientific community (Nappi *et al.* 2004) with terms such as "destroyed", "damaged", and "lost" being used to describe burned areas (Lindenmayer and Noss 2006). It is becoming increasingly understood however that salvage does not aid ecosystem recovery as previously assumed (Schmiegelow *et al.* 2006) but instead has many negative effects on both the biotic and abiotic environment (Lindenmayer 2006). It has even been identified by some as a double disturbance

(Greene *et al.* 2006; Lindenmayer 2006; Lindenmayer and Noss 2006) that places additional stress on recovering ecosystems, and especially on those species that have adapted to the fire regime but not to fast multiple disturbances (Lindenmayer 2006).

Fire is part of the boreal forest system and allows for the persistence of certain species all of whom have adapted, to greater or leer extant, to this type of disturbance (Lindenmayer and Noss 2006). The effect of this relatively new harvest technique is poorly understood (Greene *et al.* 2006; Lindenmayer 2006), and thus has few ecologically-oriented guidelines have been developed to reduce ecosystem damage (Morissette *et al.* 2002). The few studies conducted thus far have focused on animals (St. Germain and Greene, 2009; Greene *et al.* 2006) with, to our knowledge, only one directly related to plant recruitment by Greene *et al.* (2006).

Salvage has many negative effects on tree recruitment. It removes all economically viable timber that is accessible and can therefore be more intensive and extensive that traditional timber harvest techniques (Lindenmayer and Noss 2006). By removing the trees, the seed source is also effectively removed (Greene *et al.* 2006; Schmiegelow *et al.* 2006) resulting in a decrease in the recruitment of the conifer species with aerial seedbanks. In a study on post-salvage tree recruitment Greene *et al.* (2006) found that black spruce had four times less regeneration in salvaged sites than non-salvaged sites while jack pine had five times less. This was attributed primarily to removal of the aerial seedbank, and secondarily to the lessened shade in the salvage site. This reduction of conifer regeneration can lead to a shift in tree species composition, specifically from conifer dominated to hardwood dominated forests (Greene *et al.* 2006) as species such as aspen and paper birch take advantage of salvage conditions. Similar

observations have been made over a much longer interval in areas subjected to traditional harvesting (i.e. clearcutting of intact stands) (Greene *et al.* 2006).

Salvage operations also affect seedbed frequency and distribution. Greene *et al.* (2006) found that skid paths made mineral soil five times more common in salvaged than in non-salvaged sites, and solid wood (mainly branches and chips) six times more common than in non-salvaged sites. Surviving (i.e. green) *Sphagnum* was only found in non-salvaged sites.

The removal of standing trees and the disruption of the forest floor due to salvage operations leads to more open conditions. This leads to more solar radiation reaching the ground and faster rates of evaporation thus, it has been speculated, leading to drier seedbeds that are less favorable to germination and survivorship (Greene *et al.* 2006; Calogeropoulos *et al.* 2004; Schmiegelow *et al.* 2006).

Salvage logging also has many negative effects on species composition and populations (Lindenmayer 2006), on aquatic ecosystems (Lindenmayer and Noss 2006); soil formation (Greene *et al.* 2006) and nutrient cycling (Lindenmayer and Noss 2006). It can lead to exotic species invasion along newly constructed roads, as well as increased rates of erosion and stream sedimentation (Lindenmayer and Noss 2006).

Burnt areas attract certain plants and animals that rely on habitat episodically created by fire (Lindenmayer and Noss 2006; Morissette *et al.* 2002). For example, charred trees and logs attract wood boring beetles (Morissette *et al.* 2002) that, in turn, provide food for woodpeckers (Farris and Zack 2005). These standing charred trees also provide nesting sites in the form of cavities for mammals, birds, reptiles, invertebrates and amphibians (Farris and Zack 2005), perches for birds of prey and carnivorous

mammals, and habitat for bryophytes (Lindenmayer and Noss 2006). Schmiegelow *et al.* (2006) observed that woodpeckers, usually common in recently burned areas, were absent from salvaged areas. Many species also exhibit a preference for larger snags (Farris and Zack 2005), which are targeted in salvage operations. Salvage has also resulted in positive or neutral effects on biota, but only for species that benefit from open conditions (Lindenmayer and Noss 2006).

This thesis is composed of three chapters focusing on the post-fire regeneration dynamics of black spruce and jack pine following salvage. The first examines the effects of snow on the compaction of the organic layer and thus on the suitability of the substrate for germination; The second chapter examines the abscission schedule of black spruce and jack pine, which is crucial in understanding the timing of post-fire recruitment; The third and final chapter outlines a post-fire and post-salvage recruitment model which uses the abscission schedule from chapter 2 as well as other data to examine the effects of salvage on seedbeds, seedling densities, and seedling age structures .

Chapter 1 Does the post-fire organic layer compress beneath the snowpack?

Introduction

Fire is the dominant natural disturbance in the boreal forest of North America (Johnson 1992), and its effect on seedbeds, via duff consumption, has been of abiding interest (Lutz 1956; Dyrness and Norum 1983; Miyanishi 2001; Miyanishi and Johnson 2002). The great majority of boreal plant species have small seeds (0.1 to 20 mg) and necessarily therefore have small germinants. In turn, the bulk of these short germinants are found in the areas of very thin (or absent) post-fire char (Charron and Greene 2002; Greene *et al.* 2007; Johnstone and Chapin 2006) as these are the only spots where capillary water will be abundant. The organic layer thickness is quite patchy at the scale of 0.5 meters; both Miyanishi and Johnson (2002) and Greene *et al.* (2007) have likened the immediate post-fire substrate to a matrix of charred but quite thick duff (barely reduced in depth by the smoldering combustion) containing a few well-combusted patches. These "holes" tend to be centered on burnt boles and large surface rocks (Greene *et al.* 2007). The small-scale spatial heterogeneity is certainly more complex when water is abundant at the time of fire such as in bogs or where permafrost is present (Benscoter and Weider 2003; Kasischke and Johnstone 2005).

Both Johnstone and Chapin (2006) and Greene *et al.* (2007) have shown that early survivorship of tree germinants is inversely proportional to post-fire duff depth, although the relationship is non-linear. Generally, for the small germinants of boreal tree species, the initial (seedbed-mediated) survivorship for the organic layer depth class 0-3 cm is quite high, while the subsequent decline in survivorship with depth becomes precipitous at organic depths much greater than 5 cm (*Greene et al.* 2007; Miyanishi and Johnson

2002; Johnstone and Chapin 2006). This functional relationship is ultimately mediated by the ratio of radicle length (dependent on seed size) to the depth of the porous, easily-dried duff. One wonders: would the snowpack following the first summer sufficiently compress the post-fire duff layer so that (at least) the intermediate post-fire depth classes of, say, 3-10 cm would become more suitable for germination?

One reason to think that the compression by snow might play a role involves a temporal pattern in post-fire germination success that has been reported three times in experiments where sowing permitted an investigator to hold seed input constant. Thomas and Wein (1985), Charron and Greene (2002), and Kemball *et al.* (2006) used sowing experiments to show that the germination of black spruce (*Picea mariana*) and jack pine (*Pinus banksiana*) was much greater in the second and third summer than in the first summer following fire. They hypothesized that this temporal pattern was primarily due to the leaching of the thick first-summer ash layer. We provide an alternate argument: much of the burnt organic layer is not sufficiently dense to retain adequate moisture in the first summer or two following fire, but subsequently, via the compaction due to a snow layer, the porosity is decreased thereby sufficiently elevating the moisture content in the germinant rooting zone (a few cm depth).

We have found no studies on the effect of the initial snowpack on subsequent post-fire organic layer thickness, and yet it makes sense that the layer could well be compressed by snow. Anecdotally, when one walks across first-summer burnt duff, the charred fibers do not merely audibly crunch beneath one's boots; the prints remain deep and well-outlined months later. This is not surprising: the charred duff fibers are quite brittle. Likewise, we have repeatedly observed that the clearly-defined hoof-prints of deer

and moose in freshly-burnt duff become favorable substrates for moss spore establishment the next summer presumably because they are much less porous than the adjacent burnt duff. It could also be that modest shading by the steep "walls" of the print would significantly reduce evapotranspiration. Csotonyi and Addicott (2004) observed this same effect of ungulate hoofprints for the moss *Ceratodon purpureus*, although this was on unburnt silt-rich dune substrates.

The objective of this study was to determine whether the snow in the first three years following fire significantly compacted the organic seedbeds. This was done by re-measurement of the height of the organic material along lengths of rebar whose lower ends had been hammered deep into the mineral soil.

Methods

The Mistissini fire, where our stands were located, occurred in northwestern Quebec approximately 17 km east of the community of Mistissini (50° 21' N, 73° 41' W). Ignited by lightning in the first week of June 2006, it burned 920 ha of forest before it was extinguished by rain a few weeks later.

Two stands on flat ground well away from water bodies, each with 100% tree mortality, were selected within the burn, and then marked off in agreement with the companies performing the subsequent salvage operation. One stand had been dominated by black spruce before the fire and the other by jack pine. Both were located more than 100 m from the burn edge.

Post-fire ground cover in the jack pine stand consisted primarily of charred feather mosses and lichens. Judging from nearby unburnt stands, the feathermosses had

been primarily *Ptilium crista-castrensis*, *Hylocomium splendens*, *Pleurozium schreberi*, and *Dicranum* spp., while the lichen were mainly *Cladina* spp. Ground cover in the black spruce stand, a much wetter site, consisted primarily of burnt feathermosses and, especially, burnt *Sphagnum* spp. It had a greater variation in seedbed depth and type due to a thicker pre-fire organic layer. Some of the *Sphagnum* had survived the smoldering combustion; i.e. at least some of the setae within a mound were green; we placed no rebar in those microsites. Vegetatively-regenerating *Vaccinium* spp. and *Kalmia angustifolia* were common at this site.

Two intact stands were selected to act as controls. These stands were also located on flat ground far from water bodies and within 4 km of the Mistissini fire edge. One stand was dominated by black spruce and the other by jack pine. Both had a ground cover similar to the assumed pre-fire cover of our burnt stands

About one week after the fire was declared extinguished (June 24, 2006), we began the study at these 4 stands by pounding 3-m lengths of rebar a minimum of 2.4 m into a variety of substrates (burnt duff, charred dead feathermoss or *Sphagnum*, and charred lichen). The depth of the lower part of the rebar was below the level at which it might be affected by frost heaving. We can be certain that no frost heaving occurred because none of the rebar pieces had departed from the vertical when they were re-examined each summer. Each rebar piece was hit with a sledgehammer from a ladder so that the substrate around the insertion point was unaffected. Altogether, we had 6 lengths of rebar in each of the burnt stands and 3 lengths in each intact stand. One of the rebar lengths in the black spruce control site was lost due to an unexpected salvage operation.

After the initial positioning of the rebar in 2006, data on forest floor compression were obtained in the summers of 2007 and 2008 by measuring the distance from the substrate to the top of the rebar post to the nearest mm. Depth of the organic substrate (from the top to mineral soil) was measured in the final summer, and the amount of the organic layer thickness lost to compression was added to the present organic layer thickness for a subsequent calculation of the total amount of compression as a function of the original thickness.

Results

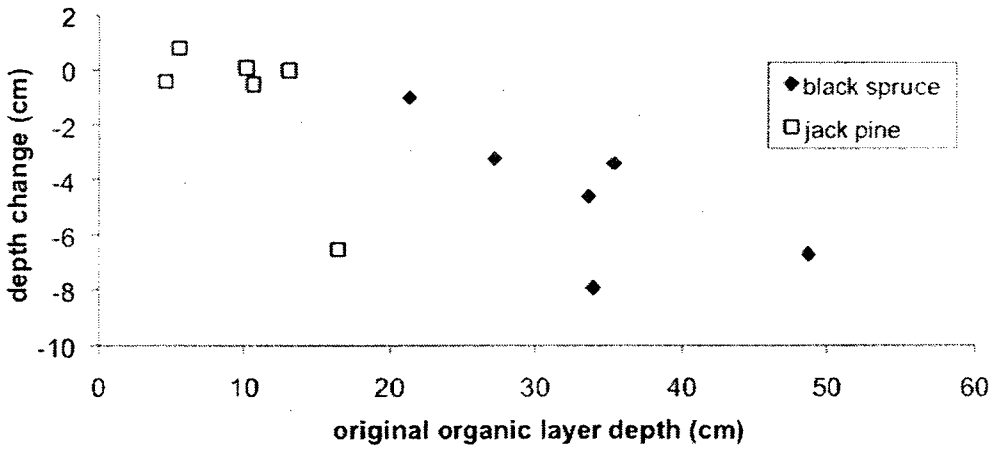
In the winter of 2006-2007 our study area received its first snowfall on October 28th. Continuous snow cover began on December 2nd and remained until April 27th. The region experienced its last snowfall on May 20th. The maximum depth of the snowpack for this winter season was 50 cm, and this was reached on March 21st. In the second winter (2007-2008) the first snowfall occurred on October 12th. Continuous snow cover began on November 6th and remained until April 24th. The region experienced its last snowfall on May 29th. The maximum depth of the snowpack was 71 cm, reached on April 2nd. These maximum snow depths were somewhat less than the long term normal (80 cm). Snow depths were obtained from local weather stations.

From 2006 to 2008 (two snowpacks) the burnt duff compressed an average of 2.8 cm (σ=3.0 cm), with each of the two winters accounting for an equal amount of compression. The amount of substrate thinning for the 12 rebar pieces in the burnt sites was significantly different from 0 (1-sample t-test; p=0.009; df=11). By contrast, the intact duff in the control compressed by an insignificant amount (0.12 cm; σ=1.29 cm;

p>0.85; df=4). Given the small sample sizes and large standard deviations, the two-sample t-test comparing compression for the burnt vs. intact stands was only barely significant despite the large difference in the mean amount of compression (p=0.042; df=15).

Figure 1 depicts the highly significant negative relationship between the post-fire reduction in organic layer thickness and the initial thickness of the organic layer just after the fire (r^2=0.67; n=12; p=0.0007). Given that the intercept (1.3) was not significantly different from 0, we performed the regression a second time but with the intercept now held constant at 0. The new slope was -0.14 (r^2=0.72; p=0.00004). That is, there was an estimated 14% compression of the organic layer after two winters.

Figure. 1. Thickness of the burnt organic layer immediately after the fire vs. the total change (cm) in thickness after two winters in two burnt stands. A negative value indicates substrate compression.



The qūestion arises whether the relationship in Figure 1 reflects primarily a difference between the jack pine and black spruce stands, granted the much greater organic depths at the latter site. Separate correlations (with the intercept set to zero, and n=6 for each) for the two burnt stands revealed an almost significant negative correlation for the jack pine rebar lengths (p=0.067) and a significant negative relationship for the

black spruce rebar (p=0.003), with very similar slopes (-0.16 and -0.14, respectively; neither significantly different from the other via a t-test). In short, irrespective of pre-fire stand composition and substrate differences, about 14% of the original thickness was lost after two winters.

Generally, within the stand, and more specifically at the foot of each of the 12 rebar pieces in the burn, there was essentially no leaf litter accumulation from recruiting plants. Accumulation of burnt needles was minor because most had been reduced to ash by the flaming combustion. That is, our results were not affected by the accrual of organic material. Sample sizes were too small to permit comparison of burnt substrate types (e.g. *Sphagnum* vs. lichen). Similarly, we hesitate to look at the joint effect of substrate type and initial post-fire depth.

Discussion

In the southern boreal forest, stand-replacing fires in May and June, such as the one we examined, accounts for 75% of the annual total area burned. The two maximum snow pack depths for the period of our study were smaller than average but not excessively so. The results seen here therefore are likely quite general. The post-fire substrates we examined with rebar clearly became thinner with time. Roughly 7% of the thickness has been lost after each of the two winters for a cumulative thinning of 14%. We could detect no difference in the compression rate due to pre-fire stand composition or initial post-fire organic layer thickness.

It is certainly possible to interpret Figure 1 more finely. Although we have too few data points to entertain separate regressions, it would seem that there was essentially

no change in depth for substrates <13 cm in thickness. If correct, the obvious interpretation is that the thicker seedbeds had, reasonably, much higher proportions of fibric material while the thinner substrates were dominated by the now-exposed, high-density humic layer. If so, it is likely that compression would be occurring only within the low-density fibric layer, and therefore only on the thicker substrates. We made no bulk density measurements at the close of the experiment, but the foregoing is certainly a reasonable interpretation of the compression results.

We have no direct proof that the observed compression was due to the weight of the snow rather than to decomposition. However, studies on decomposition and soil respiration rates following disturbance indicate that decomposition rates after a severe fire, such as the one we examined, are quite low for the first few years (reviewed in Neary *et al.* 1999). This is because the low decomposer abundance immediately after a fire initially outweighs the otherwise beneficial effects of warmer soils, especially within the dry, charred duff (Amiro *et al.* 2003; Bergner 2004; Neary *et al.* 1999). Further, Anderson (1991) pointed out that high substrate temperatures and lessened water availability after disturbance (due to lessened shade and albedo), inhibits decomposition rates. We conclude therefore that decomposition was not responsible for the charred duff compression that we observed.

Nonetheless, the modest reduction in duff depth observed after two winters cannot matter greatly for germination success. Following Johnstone and Chapin (2006) and Greene *et al.* (2007), the small germinants characteristic of boreal species have their highest juvenile survivorship (seed to end-of-summer germinant) in the duff depth interval 0-3 cm, with a sharply lower juvenile survivorship at thicknesses of 3-5 cm, and

then a survivorship of essentially 0 for depths greater than 5 cm. Thus, a 15 cm immediate post-fire depth might be reduced by 2.1 cm (i.e., a 14% loss as in our regression result), but the resulting 12.9 cm substrate thickness would remain essentially lethal (Figure 1). For the same reason the clemency of the portion of the fire with very thin post-fire substrates (say, 2 cm) would hardly be affected by a 0.3 cm decrease (14%) in depth over two years (Figure 1). In any case, if we regard the thin post-fire substrates as being comprised essentially of high-density humus that cannot be seriously compressed by snow (see the discussion above), then it follows that the optimal seedbeds (<5 cm thickness) of Greene *et al.* (2007) were precisely those which cannot be compressed any further by snow.

Of course, while substrate depths should not be dichotomized into good or bad as in this example, nonetheless the result is instructive—the weight of the snow is too small to create a substantial increase in the suitability of post-fire seedbeds. Thus, compression of charred duff due to repeated snow packs cannot be the explanation for the tendency to have a smaller-than-expected cohort for boreal tree species in the summer of the fire. Arguments about the inhibitive effects of ash (Thomas and Wein 1985; Kemball *et al.* 2006) remain the most compelling explanation for the often-observed initial post-fire lag in recruitment.

As mentioned in the introduction, the permanent depression of the brittle charred duff by a footprint is obvious to anyone who has walked around a very fresh burn. We made a small number of quantitative measurements: the depth of the prints averaged 4 cm. Why does the compression of the snowpack create, in contrast, such a modest effect? We can roughly estimate the pressure applied by an adult human. Assuming a

boot sole area of around 0.015 m^2, a gravitational acceleration of 9.81 m s^{-2}, and a mass of 100 kg, then, the pressure on the charred duff would be about 65,000 Pa. By contrast, even old snow where freeze-thaw episodes have increased the density to say 300 kg m^{-3}, would, with a depth of 1 m, only supply a pressure of about 3000 Pa. In short, there is more than an order of magnitude difference in the pressure applied by an adult human and by the snowpack, and thus the compression of the brittle duff by the former would be, correspondingly, far greater. We conclude that our initial hypothesis, based on the compression created by a bipedal scientist, was a poor guide to what snow might achieve.

In salvage operations in the boreal forest, we expect that the compaction due to the harvesting equipment would be even more dramatic than that due to the weight of an adult human. Nonetheless, this will not greatly ameliorate the typically poor post-fire recruitment (Lindenmayer *et al.* 2004) for a number of reasons. First, with a careful harvesting system such as CPRS (Coupe avec Protection de la Regeneration et des Sols), about 30% of the ground will remain unaffected by the heavy equipment. More importantly, the dryness of the substrates (due to the loss of shade-providing standing burnt trees) and the dearth of seeds (due to the loss of seed-bearing branches for those species with aerial seedbanks) are the main reasons for the much lower numbers of seedlings found in salvaged boreal sites (Greene *et al.* 2006), and these two factors undoubtedly greatly outweigh the positive effect of the compression caused by machines.

Chapter 2 Post-fire seed abscission schedule of *Picea mariana* and *Pinus banksiana*

Introduction

The species composition of boreal forest communities is highly dependant on large fires, the dominant disturbance type (Johnson 1992; Payette 1992). Approximately 97% of the annual area burned is comprised of large (>200 ha) stand-replacing crown fires (Amiro *et al.* 2001; Stocks *et al.* 2002). A relatively short fire return interval of 50-150 years (Johnstone *et al.* 2004) has resulted in the regional dominance of fire-adapted tree species (Enright *et al.* 1998; Lindenmayer and Noss 2006). As an example, the distribution of jack pine (*Pinus banksiana*) is closely tied to fire (Gauthier *et al.* 1993*b*;De Groot *et al.* 2004; Asselin *et al.* 2003; Scherer-Lorenzen *et al.* 2005).

The three most common tree species in the boreal forest are black spruce (*Picea mariana*), jack pine, and trembling aspen (*Populus tremuloides*) (Greene *et al.* 1999; De Groot *et al.* 2004). Their domination results largely from their ability to quickly colonize burned areas—the first two species by aerial seedbanks and the third by reliable and copious root suckers. Soil seedbanks are unimportant in the boreal forest because they are consumed by smoldering combustion of the duff layer (Greene and Johnson 1999). Likewise, the perennating above-ground tissues of shade-tolerant saplings are invariably killed by flaming combustion). Precisely because the three most common tree species are fire-adapted, and because the density of regeneration is dependent upon the pre-fire tree density, a burn confirms the pre-fire species composition: there is, for these three species, no dramatic post-disturbance change (Greene and Johnson 1999; Ilisson and Chen 2009).

The two species of interest in this study, black spruce and jack pine, have wind-dispersed seeds, a mode of dispersal made more efficient by fire as the removal of

needles, leaves and small-diameter shoots increases the ambient wind speed (Lamont *et al.* 1991). These two species retain closed cones in the canopy for several years, thus maintaining many seed cohorts on their branches (Gauthier *et al.* 1993*a*). Evolutionarily, this is an advantage for species found in areas dominated by a short fire return interval (De Groot *et al.* 2004; Lamont *et al.* 1991); indeed if fire return intervals typically exceed a species' average pre-senescence lifespan, aerial seedbanks are not an effective strategy (Lamont *et al.* 1991).

Black spruce usually has 3 to 6 seed cohorts on its branches while jack pine can have 10 or more (Enright *et al.* 1998; Greene and Johnson 1999; Greene *et al.* 1999). With increasing time on the branches, however, mean seed viability declines. Indeed, Greene and Johnson (1999) argued that the mean number of viable seeds on a tree of either species was about equal to the mean annual seed production of a non-aerial seedbank species due to relatively poor annual seed production by these two species as well as the on-going decline in viability with time.

Although, in the absence of fire, old cones of jack pine will slowly open when exposed to intense solar radiation, the great majority of cones are opened by the heat from flaming combustion as the resin bonds are melted (Enright *et al.* 1998; Lamont *et al.* 1991). For jack pine, generally, exterior temperatures >50° C are needed to open the cones (De Groot *et al.* 2004; Gauthier *et al.* 1993*a*). Black spruce will release all its seeds within a few years regardless of fire (Enright *et al.* 1998; Greene *et al.* 1999), although Zasada (1979) in Alaska argued that cone opening in black spruce was modestly accelerated by fire. Methods for studying seed abscission have mostly been indirect. Charron and Greene (2002) measured remaining seeds per cone on branches along a

chronosequence of stands with different times since fire. Others have extrapolated seed abscission rates from seedling ages although the problem of obtaining accurate seedling ages for slow-growing species makes this approach problematic (St. Pierre *et al.* 1992; Sirois and Payette 1989; Cayford 1963; Charron and Greene 2002).

We know of only two direct studies of abscission on these two species, both limited in the time span they cover. Johnstone *et al.* (2009) used seed traps to examine black spruce seed rain and viability over a two year period following a late summer fire (August 2004) in Alaska, however data collection only began in June of 2005; the crucial first ten months after fire were missing. De Groot et al (2004) used traps to follow the abscission of jack pine seeds only for the first 2 to 3 months following an experimental fire.

The deleterious effects of post-fire salvage on aerial seedbank species are intimately related to the timing of seed abscission. The few indirect studies of the timing of post-fire seed abscission of aerial seedbank species in the boreal forest (mentioned above) indicate that the rate is faster for jack pine than black spruce (Charron and Greene 2002). More specifically, jack pine abscission begins immediately following fire (De Groot *et al.* 2004) with cones emptied within 3 years (Greene *et al.* 2004). As examples: two years following fire, jack pine had 3% of the seeds remaining in its cones and after four years had only 0.8% while black spruce had 35% and 6%, respectively (Charron and Greene 2002).

Salvage of burned stands after fire is increasingly used to offset the economic loss resulting from otherwise foregone future harvests (Lindenmayer and Noss 2006; Greene *et al.* 2004). Typically, salvage occurs as fast as possible, usually in the first winter after

the summer fire, because foresters wish to (1) prevent damage to the timber from wood-boring beetles; (2) reduce checks (wood splitting) that typically develop as the standing dead trees dry; and (3) given windthrow, enhance the number of burnt trees that will still be standing when the harvesting machinery passes by (St. Germain and Greene 2009).

As a result of quick salvage, large numbers of cone-bearing trees of black spruce and jack pine still have many non-abscised seeds at the time of harvest. These seed-bearing cones are either deposited in slash piles at the edges of roads or end up on the ground where they cannot disperse their seeds widely (Greene *et al.* 2004; Lindenmayer and Noss 2006). It may be presumed that the problem will be less serious for the rapidly-abscising jack pine than for black spruce. In any case, a delay in salvage would benefit the regeneration potential of either species as it would lead to a greater percentage of seeds abscising prior to the harvest (although of course if the delay was too long, this enhancement of recruit density would be partially offset by the trampling of the first-summer germinant cohort on the skid paths by machinery). In turn, this would reduce the amount of post-fire planting required. But our ability to quantify the trade-off in the salvage timing—planting cost vs. lost wood value—is hampered by our lack of detailed knowledge of the abscission schedule of these two common boreal species.

We examined seed release of black spruce and jack pine in the first three years following two stand-replacing fires in northwestern Quebec. Our goal was to determine whether the rough inferences from studies of cones and seedling ages—most seeds of jack pine abscising within two years with the schedule for black spruce lagging perhaps one or two years behind—were correct. Ultimately, however, our aim was to understand at a fine time scale how current salvage techniques affect the ability of these species to

regenerate, and therefore to be in a position to suggest changes in the present approach to salvage that would minimize some of the negative effects of removing burnt trees too rapidly.

Methods

We examined the abscission schedule in two fires: Senneterre (2007) and Mistissini (2006). The Senneterre fire was located in northwestern Quebec (48° 16' N, 76° 38' W) approximately 100 km east of the town of Senneterre. Originally, two separate fires were ignited by lightning: fire # 193 on the 14 May 2007 and fire 254 a few days after. On May 24 these fires joined together. Reaching a total area of 64,450 ha of forest burned, it was extinguished by rain in early June 2007. Two stands, each with 100% mortality, were selected within the burn, marked off, and intended to be protected from salvage. One was dominated by black spruce before the fire and the other by jack pine. Both were located more than 100 m from a burn edge.

The Mistissini fire was located in northwestern Quebec 17 km east of the community of Mistissini (50° 21' N, 73° 41' W). Ignited by lightning in the first week of June 2006, it burned 920 ha of forest before it was extinguished by rain on the 24th of June. Two stands, each with 100% mortality, were selected within this burn, marked off, and intended to be protected from salvage. One stand had been dominated by black spruce before the fire and the other by jack pine. Again, both were located more than 100 m from a burn edge.

Trees in the black spruce stands were about 13 m tall whereas trees in the jack pine stands averaged 16 m. Post-fire ground cover in the black spruce stands was made

up of burnt duff, feathermosses (*Ptilium crista-castrensis*, *Hylocomium splendens*, *Pleurozium schreberi*, and *Dicranum spp)*, and *Sphagnum spp.* In the jack pine stands, post-fire ground cover was dominated by burnt duff, feathermosses and lichens (mostly *Cladina spp*). The vegetatively-regenerating shrubs *Vaccinium spp* and *Kalmia angustifolia* were also common in both stands.

We installed seedtraps one week after the fire was extinguished. Soil samples were taken using a coring tube prior to trap installation to ensure that seeds already fallen on the burnt duff prior to trap installation could be accounted for. The tube was inserted into the substrate next to the newly-installed seedtrap until it reached mineral soil; the core was then extracted. The tube contents were dried in a lab; after sieving, the total number of spruce and pine seeds for cores/site was determined. One hundred samples were taken from each site (core aperture area = 12.6 cm^2), for a total area of 0.126 m^2 per stand.

We used two types of seedtraps: In the stands at the Senneterre fire box seedtraps were used for the entire experiment. In the Mistissini fire for the first two years plastic cup seedtraps were used. However, we switched to box seedtraps in the final year of study. The plastic cups, with an area of 33.18 cm^2, were spaced 0.5 m from one another in a 10 by 10 array, these 100 cups providing a total area of 0.33 m^2. Each trap consisted of two cups: the bottom was cut out of one cup and replaced by landscape fabric, which was then inserted into the second cup. The landscape fabric "Weed Stop", manufactured by Spectrum Brands IP Inc. was highly porous and durable, thereby minimizing damage to seeds from being submerged in standing water.

We built the boxes of wood and lined them with landscape fabric to minimize water damage to seeds; they were elevated to minimize access to rodents. The wooden frame measured 50 by 100 cm. Four to five of these traps were placed randomly in each stand.

We obtained data in the summers of 2006 through 2008 for Mistissini and 2007 through 2009 for Senneterre. Traps were checked and seeds collected and counted three times each year: late-spring, mid-summer, and late-summer. At each site the sum of all seeds found in the traps was recorded. Broken or frost-heaved cups, and boxes broken by falling boles were replaced or repaired when necessary. The landscape fabric was replaced annually. In the summer of 2008 (Mistissini) and 2009 (Senneterre), upon our final visit to each respective site, 10 cones of black spruce and jack pine were taken from 10 separate trees for a total of 100 cones per site. The remaining filled seeds within these cones were counted after drying at room temperature for several months to determine the final number of full-sized seeds not yet abscised. Based on the imprint of full-sized seeds on the scales of these cones we also estimated the original number of filled seeds available at the time of fire.

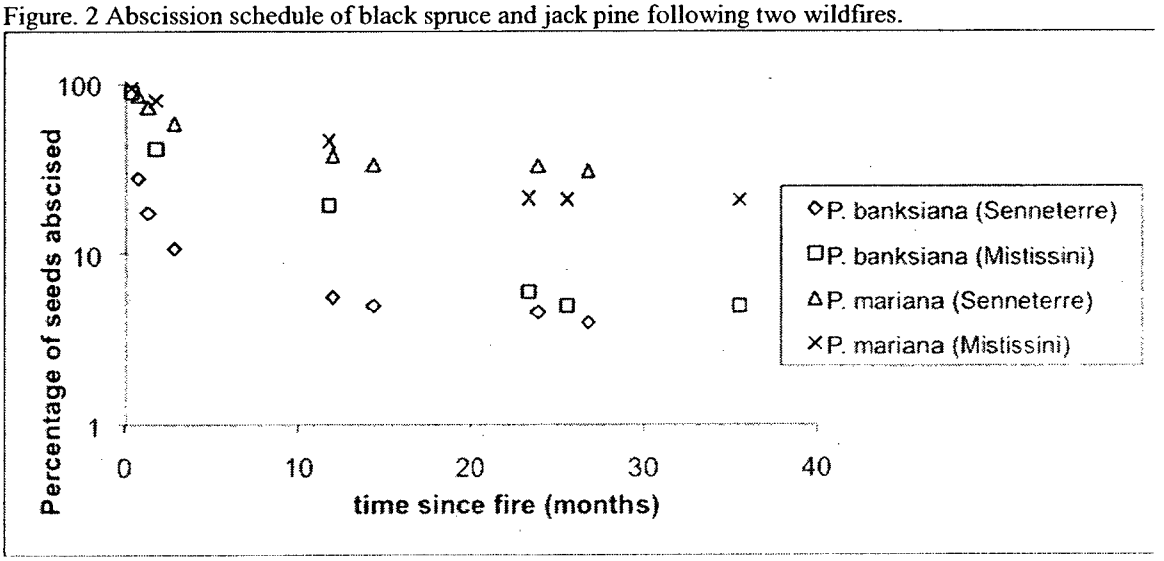
Results

The abscission schedule of black spruce at both sites was similar (Fig. 2). Both correlations of time on proportion of seeds remaining in the cones, based on semi-log regressions with the intercept forced through the ordinate value of 100%, were significant. At Senneterre, black spruce had a slope of -0.051 whereas at Mistissini the slope was -0.043. There was no significant difference between the two slopes ($p=.433$).

Likewise, for jack pine, both semi-log correlations of time on proportion of seeds remaining were significant (Fig. 2; $p<0.05$); and there was no significant difference between the two slopes ($p=.402$). At Senneterre, the jack pine slope was -0.101 whereas at Mistissini the slope was -0.137.

Lumping sites (n=12 for both species now), the correlations for both species were significant ($p<0.005$). For these lumped data sets, however, there was a difference ($p<0.005$) in the slopes with jack pine (slope = -0.096) significantly steeper than black spruce (slope =-0.046).

Figure. 2 Abscission schedule of black spruce and jack pine following two wildfires.



Discussion

The results indicate that black spruce has a slower abscission schedule than jack pine; this is consistent with indirect observations made by Charron and Greene (2002). Approximately 1.5 months following fire, black spruce had abscised 23% of available seeds whereas jack pine had abscised 71% of its seeds. After approximately 24 months black spruce had abscised 74% of available seeds whereas jack pine had little left: about

5% of the original seed complement. These latter amounts are similar to what Charron and Greene (2002) observed with a chronosequence of seeds per cone following fire; after about 24 months they found that 65% and 97%, respectively, of the seeds had abscised from the cones.

Both species avoid potentially problematic schedules where abscission is too hurried or too delayed. It has been argued that the first-summer cohort of post-fire seeds frequently has poor survival because germination-inhibiting ash deposits are still thick (e.g. De Groot *et al.* 2004; Thomas and Wein 1985; Wang and Kemball 2005). But even jack pine by September 1, say four months following the late spring fire that typifies the southern boreal forest, would have about 30% of its crop still available for the second summer. In consequence, even a prohibitive depth of ash would not be catastrophic for jack pine. A fire occurring later in the summer would pose even fewer problems.

At the other extreme, the slow deterioration of the better seedbeds as broadleaf litter accrues (reviewed in Greene *et al.* 1999) should not deleteriously affect the more slowly-releasing black spruce. Age-specific early survivorship on the best seedbeds (exposed mineral soil and thin humus) appears to not decline seriously until about the 4th year following fire (or even later if there are few broadleaved shrubs and trees: Charron and Greene (2002)).

Our results indicate that the seasonal timing of both fire and salvage will impact the proportion of seeds available to germinate in the first summer. As previously mentioned, salvage occurs as fast as possible, usually within a few months of the fire after road construction is finished. This will not give black spruce, and to a lesser extent, jack pine, sufficient time to abscise enough seeds to adequately stock the burned stand,

thus leading to poor natural conifer regeneration and, necessarily, expensive planting (Greene *et al.* 2004). Based on our observations we suggest that salvage be delayed until the second winter following fire for black spruce stands, and until the first winter for jack pine stands. This would allow for a greater proportion of seed abscission to occur and thus greatly reduce or eliminate the costs associated with planting. The situation is certainly less neat than imagined here. We are presently developing a model that includes not only these abscission schedules and the timing of both the fire and salvage, but complications such as (1) the expected fraction of germinants killed by harvesting after a delay, and (2) the fact that skid paths are often very good seedbeds dominated by exposed mineral soil.

The quick removal of burnt trees affects not only conifer regeneration but also plants and animals that rely on these species for survival, and thus there are other, equally-compelling, reasons to delay salvage. Many animals are attracted to burnt areas; for example, charred trees are used by woodpeckers and owls, carnivorous mammals, and saprophagous beetles (Lindenmayer and Noss 2006; Nappi *et al.* 2004; Greene *et al.* 2006; St. Germain and Greene 2009). Pyrophilous ground-dwelling insects are present only for two to three years following fire. This in turn limits the concentration of fire-associated animal species to the same temporal window between fire and salvage (Saint-Germain and Greene 2009). Presumably a two to three year delay in salvage would therefore be quite beneficial for these species, and not just for the sexually-recruiting plants.

Chapter 3 A model of the post-fire recruitment of *Picea mariana* and *Pinus banksiana* as a function of salvage timing and intensity

Introduction

Fire is the dominant disturbance in the boreal forest (Johnson 1992; Payette 1992), causing significant losses in viable timber. In Canada, the fire return time ranges from 100 years in the southern boreal to 250 years in the taiga, and this has resulted in the dominance of pyrophilic species adapted to this disturbance regime (St-Germain and Greene 2009). Timber companies and governments have responded by increasingly using salvage logging to recuperate losses (Greene *et al.* 2006; Lindenmayer and Noss 2006; St-Germain and Greene 2009).

Current salvage procedures generally remove all accessible timber in a burn, and can therefore be more extensive and intensive than traditional harvest techniques where the emphasis in only on commercially valuable (i.e. the larger individuals of only certain species) stems (Lindenmayer and Noss 2006). Salvage usually occurs as rapidly as the initial road network can be constructed, typically within a few months of the fire, and is normally completed within 6 to 10 months. Companies salvage as quickly as possible because of the expected degradation due to wood-boring insects, stain fungi, wood-decay fungi, and checking (wood splitting due to drying of the timber) (St-Germain and Greene 2009). Another reason for celerity is that the standing dead trees continue to fall with time since fire, but the rate is sufficiently slow that this is not a primary concern. These degradation agents vary in their effect on wood quality and structure: wood affected by checking, stain fungi, and insect damage can still be used for pulp.

Salvage negatively impacts the natural regeneration of *Pinus mariana* and *Pinus banksiana,* two common boreal forest tree species that rely on aerial seedbanks to re-

establish after fire (Charron and Greene 2002; Greene *et al.* 2006; St-Germain and Greene 2009). Salvage removes the aerial seedbank before the majority of seeds have abscised. Further, about 30% of the first summer cohort will be crushed by the machinery (i.e. the skidpaths on which harvesters move will affect about 30% of the substrate) (Greene *et al.* 2006). Greene *et al.* (2006) observed four times less regeneration of *P. mariana* and five times less regeneration of *P. banksiana* in salvaged sites than in non-salvaged sites. They speculated that this difference was primarily due to the loss of seed-bearing cones as trees were removed from the site. They also speculated that the drier conditions in the now unshaded burn would lead to higher age-specific survivorship for germinants in the second and subsequent summers. (Nonetheless, seeds sown by Greene et al (2006) on the skidpaths had very high survivorship.) A seedling density of ~1/m^2 or greater is considered adequate to fully re-stock stands (Greene *et al.* 2002); because of salvage, natural regeneration densities of *P. mariana* and, to a lesser extent *P. banksiana,* are well below this density, and therefore forest companies are required to plant trees at an average cost of USD $750/ha (St-Germain and Greene 2009).

Suitable seedbeds, which are crucial for the successful establishment of small seeded species such as *P. mariana* and *P. banksiana* (Greene *et al.* 2006; Greene *et al.* 2007; St-Germain and Greene 2009), are affected by both fire and salvage. Fire increases the frequency of the better seedbeds by reducing organic layers (Miyanishi and Johnson 2002). It is important to note however that ash, if thick enough, has a negative impact on low porosity seedbeds in the first summer following fire; meanwhile, high porosity seedbeds are relatively unaffected as ash is leached away by rainfall at a much faster rate (Kemball *et al.* 2006). Ironically, salvage further increases the frequency of suitable

seedbeds in an area now denuded of seed sources: Greene *et al.* (2006) observed five times more mineral soil and humus (both are very favorable seedbeds) in salvaged sites because so much organic material had been pushed to the sides of the skidpath by the harvesters.

Salvage also negatively affects other species such as saproxylic beetles and woodpeckers (Lindenmayer and Noss 2006; Morissette *et al.* 2002) More than 80% of saproxylic insects (those that excavate galleries in sapwood and heartwood), and most pyrophilous ground-dwelling insects, are abundant only for two to three years following fire. This in turn limits the abundance of fire-associated woodpecker species to the same temporal window (St-Germain and Greene 2009). Unfortunately, the goal of forestry companies is to harvest as quickly as possible; i.e. to truncate the short interval in which these species build up their populations. Schmiegelow *et al.* 2006 observed, for example, that the woodpeckers usually common to burned areas were absent from recently salvaged sites.

Additional negative effects of salvage include increased rates of erosion due to tree removal, especially on steep slopes and riparian areas. Further, the increased road construction itself leads to alterations in population abundance (Lindenmayer and Noss 2006; St-Germain and Greene 2009)

Large-scale salvage is so new that current practices generally are poorly regulated (St-Germain and Greene 2009). In addition, in Canada, companies are spurred to salvage the burns by provincial rules that both require and subsidize the practice. Indeed, subsidies are almost always necessary because most of the stands will not be at the optimal size (age) to cut (St-Germain and Greene 2009).

One model currently exists that expresses post-fire tree seedling density as merely a function pre-fire seed production and the quality of the fire-induced seedbeds (Greene et al 2004). To deal with the effect of salvage however, we require a much more detailed modeling effort. Our objective is to simulate the impact of salvage timing and proportion on natural recruitment densities of two common aerial seedbank species, *P. mariana* and *P. banksiana*. We will first test the model using data from three fires in the boreal forest of North America. Then, we will use it to explore how the timing and proportion of salvage affects the subsequent recruitment density of each species. Lastly we will model the effect of redistributing seeds (by feeding cone-bearing branches into a chipper that follows the harvester) rather than hauling them offsite along with the boles.

The model

General approach

This model simulates the establishment (density) of *P. mariana* and *P. banksiana* seedlings from aerial seedbanks following fire and salvage. It models seed availability, the delay of germination until the spring, and age-specific juvenile survivorship as a function of seedbed type and proportion and ash availability. Finally, the model includes the effect of salvage timing and proportion on the seedling density. This model ignores exogenous factors such as differences in weather from one year to the next, and competition with other plant species. A major omission is that it does not include cone-bearing branches (and thus seeds) that fall onto the ground as a direct result of salvage operations; indeed, it is assumed that all branches are hauled away along with the boles. We used a simulation period of 72 months (6 years), reflecting the vast majority of both

seed abscission and post-fire sexual recruitment. The following sections address the assumptions and coupled functions of the model.

Seed availability before and during the fire

As argued empirically by Greene and Johnson (1999) for these two species in Saskatchewan, seed production per m^2 (Q_D) is directly proportional to tree basal area per area (m^2/m^2):

(1) $Q_D = 163\ 400\ (0.53)\ B_D^{0.95}$ (*P. mariana*)

(2) $Q_D = 35\ 097\ B_D^{0.86}$ (*P. banksiana*)

In equation (1) we follow Greene and Johnson (1999) in assuming that only 53% of the seeds of *P. mariana* survive passage of the flaming front while the *P. banksiana* seeds, insulated with much thicker ovulate scale, are not harmed by the fire. It is further assumed that the overlapping dispersal curves of individual trees result in a random distribution of deposited seeds in space.

Seed abscission

The seed abscission schedules of *P. mariana* and *P. banksiana* following fire were empirically documented in Chapter 2. Both species showed an approximately constant rate of abscission per month ($Q_D(t)$), and therefore the process was modeled as a negative exponential function with the intercept forced to pass through 1.0 at $t = 0$. *P. banksiana* had a much faster rate of loss than *P. mariana*:

(3) $Q_D(t) = 0.046\ e(-0.046\ t)$ (*P. mariana*)

(4) $Q_D(t) = 0.096\ e(-0.096\ t)$ *P. banksiana*)

where t is in months.

Seasonal availability of seeds for germination

While seed abscission occurs year-round, germination occurs only in the summer. This model assumes that seeds abscised from June to August are able to germinate during this period while those abscised between September and May must wait until the following summer to germinate (Greene et al, 1999).

Granivory and cumulative juvenile survivorship

Some substrates (exposed rocks, firm logs, charred logs, and standing puddles) are simply lethal and can be assigned a cumulative survivorship of 0. To calculate the cumulative survivorship (S) of a cohort over its first three summers from deposited seed to seedling, we followed the argument of Greene and Johnson (1998) and divided seedbeds into good (with proportion, w) and poor ($1-w$). Note that these two proportions sum to the total non-lethal proportion of the ground. We assumed that the survivorship on either type was dependent on germinant size, with the latter, in turn, dependent upon seed mass (m) in g. Their equation is:

$$S = gw[1 - \exp(-f_L m^b)] + g(1 - w)[1 - \exp(-f_H m^d)] \quad (5)$$

Seed mass was 0.0012 g for *P. mariana* and 0.0045 g for *P. banksiana* (Greene and Johnson 1999). The remaining empirical parameters were taken from Greene and Johnson (1998): b and d were set at 0.43 and 0.76, respectively; f_L and f_H were set at 1.83 and 0.33, respectively; and finally, g is the survivorship through the granivory stage, set at 0.53. Finally, it is assumed that after the third summer, the age-specific survivorship for any cohort is near 1.0 (Charron and Greene, 2002).

Real conditions are hardly as simple as expressed in equation (5). Certainly not all

"good" seedbeds are equally good, and some of the poor seedbeds are in fact nearly lethal (e.g. lichens). Nonetheless, the difference in survivorship between the two groups is far greater (on average, an order of magnitude greater) than among the seedbeds in a group. Temporally, age-specific granivory rates increase with time following fire as rodents reinvade the burn. However, this temporal decrease in the survivorship parameter g (probably declining from a value near 1.0 to around 0.15) would depend on distance to burn edge (Charron and Greene, 2002), and as this is not a spatially explicit model we will simply maintain the constant value $g = 0.53$ empirically obtained by Greene and Johnson (1998).

For this study the good seedbeds were similar to those of Greene et al (2006): exposed mineral soil, thin residual duff, and living (surviving) mosses. The poor seedbeds had thick residual duff or a thick layer of leaves or dead mosses, or were lichens.

Salvage affects the seedbed proportions. Greene et al. (2006) observed a 30% increase in mineral soil and thin humus in a 100% salvaged site due to organic layer removal by harvesters. All of this increase was on the skidpaths; i.e. the skidpaths occupied about 30% of the burn. In the model we reduce all pre-salvage proportions (multiplying by 0.70) and then add 0.3 to the category w. This is far too simple as in many cases the machinery is baring rocks (a lethal substrate) or creating depressions (ruts) that are filled with water part of the time (but not when we are sampling). That is, the assumption that 30% is added to the "good substrate" category is too optimistic.

The effect of ash on cumulative survivorship

In the first post-fire summer, germination rates are often unexpectedly low on

nominally good seedbeds (but never as low as on, for example, thick duff). It has been argued that this is due to the presence of substantial amounts of ash (Kemball et al. 2006; De Groot et al. 2004; Greene et al. 1999). The poor seedbeds are relatively unaffected as they are high porosity substrates, and thus the ash is leached by rainfall at a much faster rate (Kemball et al. 2006). Germination results following sowing by Kemball et al. (2006) at a burn in Manitoba were used to determine the reduction in cumulative survivorship for the conifer species on the good substrates (mineral soil and thin humus in this case) in the first summer following fire. The first year age-specific survivorship proportion for each species was reduced by 72% for *P. banksiana* in the first summer (relative to results in the second and third summer sowings) and by 98% for *P. mariana*. Thus, in the model we reduce the expected survivorship on the good seedbeds (equation (5)) by these factors for the first summer cohort only. The sparse first summer germinants on poor seedbeds were calculated as in equation (5).

Seed removal by salvage

Seeds not yet abscised at the time of salvage are removed during the harvest. Thus, if for example, 50% of the area is salvaged, then it is assumed that 50% of the remaining seeds have been removed. This is far too simple as many cone-bearing branches will be knocked off the boles during the operation, but as we have no data on the number of seeds per area inside cones remaining on-site immediately after salvage, we can only acknowledge that this aspect of our model will underestimate the recruitment density.

Seedling and seed mortality from salvage

Seedling and seed mortality results from the passing of machinery along skid paths. It is set at 30%, the percentage of the burn covered by the parallel skidpaths (Greene *et al.* 2006. i.e. if for example there were 10 germinants per m^2 after the first summer and 100% salvage occurred at some point between September and May, then the first summer cohort is reduced by 30% to 7.0 seedlings per m^2. As for seeds that fell onto the ground between September and the salvage date (and had therefore not yet germinated), these likewise were reduced by 30% because the machinery heaps the organic material into "windrows" along the two sides of the skidpath, and thus the vast majority of these seeds will be irremediably buried. When the salvage proportion is less than 1, then the mortality endured by first-summer seedlings and ungerminated seeds is reduced accordingly. Thus, for example, if 50% of the area is salvaged then the deposited (but not yet germinated) seeds and post-germination recruits seedlings are multiplied by 0.15 (i.e. 0.5 x 0.3).

Model validation

Simulated seedling densities were compared to observed densities obtained from (1) the present study conducted in the 2005 Lebel-sur-Quevillon (Quebec) wildfire (Figure 3), (2) Greene *et al.* (2006) and Greene *et al.* (2004) in the 1997 Val Paradis (Quebec) wildfire (Figure 3), and (3) Greene and Johnson (1999) for one fire in Saskatchewan.

Exploratory simulations

Exploring the model, we conducted three sets of simulations. First, we ascertained for each species the effect of delaying salvage. We ask: what is the pre-fire basal area per area that will provide adequate stocking given a100% winter salvage (December salvage)

in year *t*. The second set of simulations was like the first except we additionally asked what would be the effect of reducing salvage intensity to values less than 100% harvesting. We assumed for this second scenario that, with less than 100% salvage, residual stands will be in parallel rows and seed dispersal need not be explicitly examined. Third, we asked what would happen if cone-bearing branches were fed into a chipper that followed the harvester along the skid path and sprayed the mix of seeds and chips across the surrounding area *behind* the advancing harvester. In particular, for this third scenario we imagined that (1) the seeds are redistributed randomly across the site (including the good seedbeds created by the harvester) and (2) 75% of the residual seeds were available for redistribution, the remaining 25% being accounted for by seed mortality inside the chipper or by small branches that were not thrown into the machine.

In both simulations we assumed that the species of interest is the only component of the stand that has commercial value and figures in the stocking calculation. Further, we assumed that regeneration satisfying the minimally full stocking criterion corresponds to a minimum recruit density of 1.0 seedlings per m^2 (Greene et al, 2002). We also assumed the following post-fire (but pre-salvage) seedbed percentages: mineral soil and humus 17%, living sphagnum and feathermoss 10%, thick duff 60%, and lethal 13%. The total fraction of good seedbeds (27%) is higher than seen generally in the eastern North American boreal forest but lower than in the west (Greene *et al.* 2007).

For pre-fire basal area per area, we only examined the range 0.001 to 0.003. Below 0.001, the species is an increasingly minor component of a stand and one should not expect full stocking no matter what the prescription. Meanwhile, values >0.003 are very unlikely to be encountered, especially for *P. mariana*.

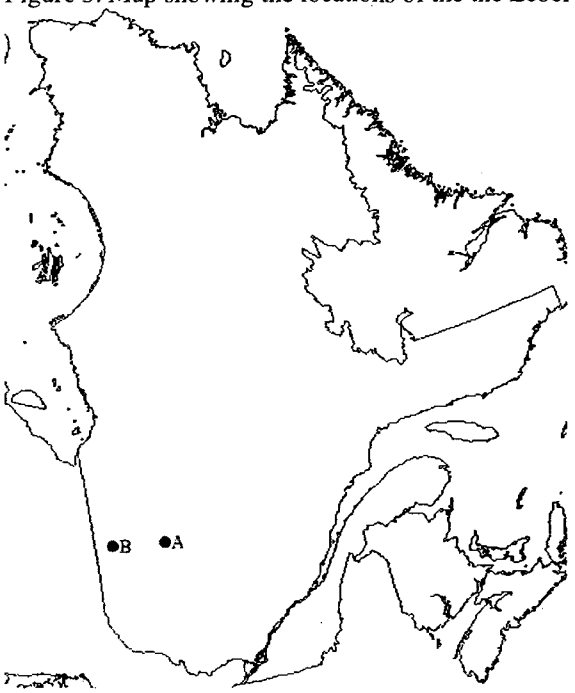
Methods at the Lebel-sur-Quevillon fire

The Lebel-sur-Quevillon fire was located in northwestern Quebec (48° 49.52' N, 77° 00.07' W) approximately 80 km from the town of Lebel-sur-Quevillon. Ignited by lightning in the early summer of 2005, it burned 4113 ha of forest until it was extinguished by rain. Salvage by the company Tembec began in October 2005 within the burn and continued until February 2006 with each month accounting for a specific area harvested. Prior to fire and salvage, selected stands within this fire were dominated by mature *P. mariana* or, more rarely, *P. banksiana*. Stands dominated by the former exhibited a large variation in organic layer depth depending on proximity to the water table; many had a ground cover dominated by *Sphagnum* while others were mantled with feathermosses (*Ptilium crista-castrensis*, *Hylocomium splendens*, *Pleurozium schreberi*, and *Dicranum* spp). The single *P. banksiana* stand had thinner and dryer seedbeds dominated by feathermosses and, in a few patches, lichens (mainly *Cladina* spp.).

Ericaceous species were common understory components in almost all the stands, and consisted mainly of *Vaccinium* spp, *Kalmia angustifolia*, *Ledum groenlandicum*, and *Gaultheria procumbens*.

All stands sampled within the burn had 100% tree mortality. Seven sites were selected within the burn; five of these within the salvaged portion, and each representing a different month of salvage (October to February). The stand representing October salvage was dominated by *P. banksiana*

Figure 3. Map showing the locations of the the Lebel-sur-Quevillon (A) and Val Paradis (B) fires.



Tembec generously granted our request to conduct a partial harvest in an area dominated by *P. mariana*. Salvage occurred in parallel strips: a 10 m wide portion of forest was salvaged leaving to the side a 10 m wide residual band. Thus, approximately 50% of the burned trees remained. One site was selected within this linear residual salvage zone for study (December salvage).

At our request, Tembec also established some areas where they did not salvage. The seventh site was located in one of these intact burned areas.

At each of the seven sites, ten randomly oriented transects were established in the summer of 2008. Each transect was 25 m long and 2 m wide. Along the transects we recorded recruit frequency, age (using budscale scars), seedbed type (based on a point every 0.5 m along the centerline of the transect; N=51 per transect), seedbed type at the base of each recruit, and basal area for any bole more than 50% within the transect. Basal area was recorded at breast height in the burned intact stand whereas in the 100%

salvaged stands it was recorded using tree stumps. In the linear residual stands both stumps and standing burned trees were included. Stump diameters were converted to the slightly smaller breast height diameters using the regression in Greene et al (2006).

Seedbed proportions (lethal; *w*; and 1-*w* for the non-lethal proportion) were determined using field data from the Lebel-sur-Quevillon wildfire. These seedbed data were obtained from a burned intact black spruce site using transects. Seedbed data were unavailable for burned intact *P. banksiana* stands; therefore, we substituted the values from the burned intact *P. mariana* site.

At Lebel-sur-Quevillon for the simulations, we assumed a salvage date of 6 months after fire. This value represented a mean among the five salvaged sites.

Results

The Lebel-sur-Quevillon fire

P. mariana seedling densities averaged 1.02/m^2 in a non-salvaged site, 0.23/m^2 in the linear residuals site (~50% salvaged), and 0.09/m^2 in a 100% salvaged site. *P. banksiana* seedling densities averaged 1.16/m^2 in the single, pine-dominated 100% salvaged site.

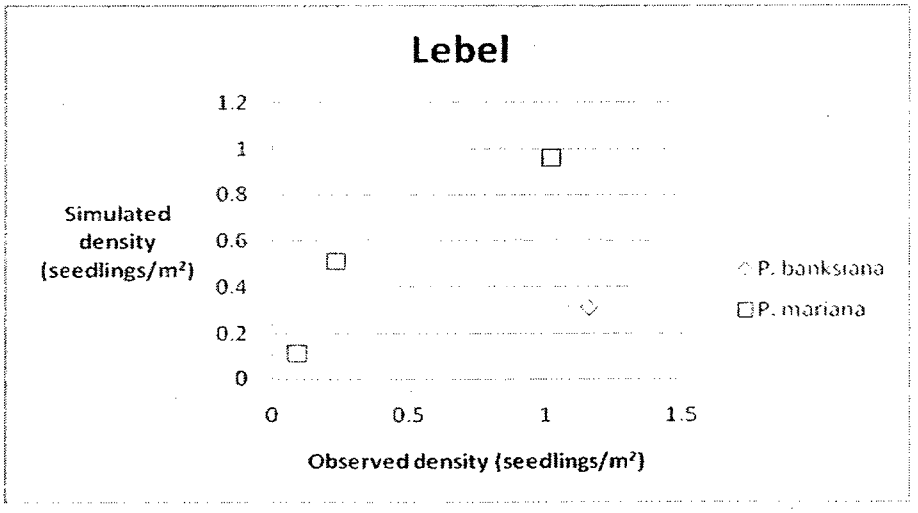
Seedbed proportions used in the model were obtained from the burned unsalvaged stand at the Lebel-sur-Quevillon wildfire. Post-fire exposed mineral soil and thin humus simply did not occur at this low-lying site. Living *Sphagnum* and feathermoss were relatively common with 11% coverage, while thick duff and dead mosses accounted for 76%. Lethal seedbeds (almost entirely charred or unburned but firm wood, the latter resulting from the splintering of wood during cutting) comprised 13% of the ground.

Prefire basal area/area averaged 0.0015 m^2/m^2 for both the burned unsalvaged *P. mariana* stand and the 100% salvaged *P. banksiana* stand, and 0.001 for both the 50% salvaged stand and 100% salvaged *P. mariana* stands.

Model validation

Simulated natural regeneration densities of *P. mariana* from non-salvaged, salvaged (100%) and partially salvaged (50%) treatments were reasonably well predicted by the simulations (Figure 4). The relationship between the observed and predicted seedling densities was strong (r^2 = 0.77) but, unsurprisingly, not significant (p = 0.22) with n=3. By contrast, the simulation underpredicted the *P. banksiana* seedling density (100% salvaged burn) by almost 4 times.

Figure 4. Observed vs simulated Lebel-sur-Quevillon *P. mariana* and *P. banksiana* seedling densities based on treatment

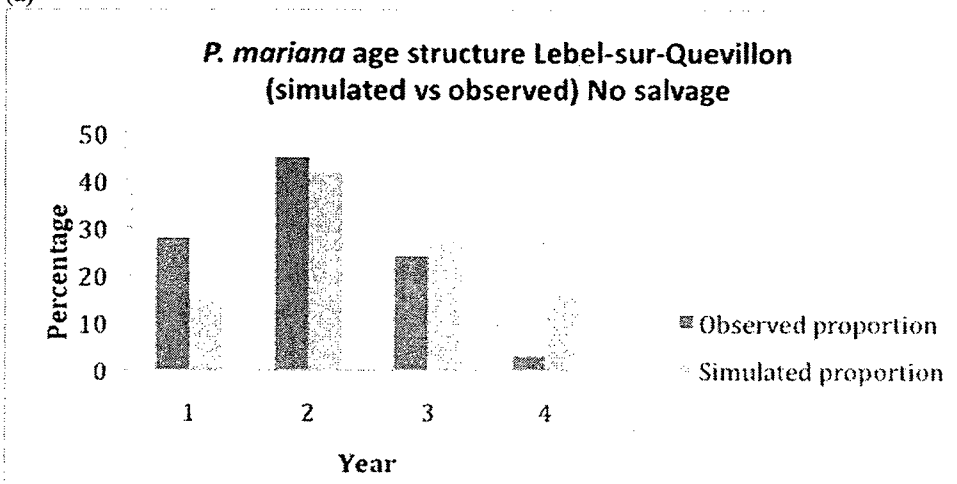


Turning to the age structure, the model under-predicted the relative size of the first-summer cohort of *P. mariana* for 0 (Figure 5a) and 50% (Figure 5b) salvage but over-predicted for 100% salvage (Figure 5c). Interestingly, in the 100% salvage treatment, about 20% of all seedlings were from the third and fourth summers; a result that the model finds impossible because it assumes all seeds are removed when salvage

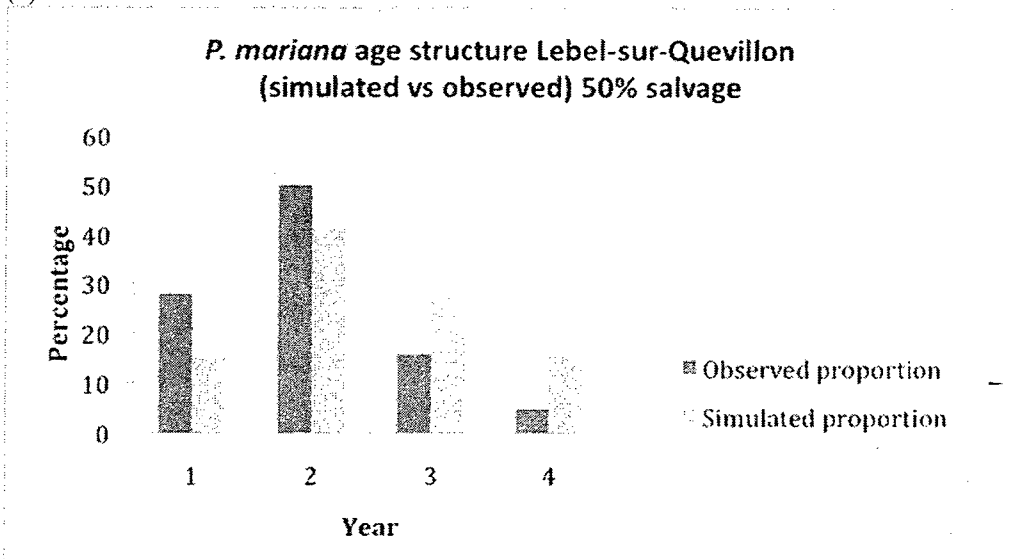
occurs, therefore no new seeds would be available for germination in the third and fourth year following fire. As for *P. banksiana* at the 100% salvage site (Figure 5d, the model again greatly over-predicted the relative size of the first cohort and was incapable of predicting the existence of the observed third summer cohort.

Figure 5. Observed *P. mariana* age structure from Lebel-sur-Quevillon vs simulated age structure (No salvage) (a); 50% salvage (b); 100% salvage (c); and observed *P. banksiana* age structure from Lebel-sur-Quevillon vs simulated age structure (100% salvage) (d).

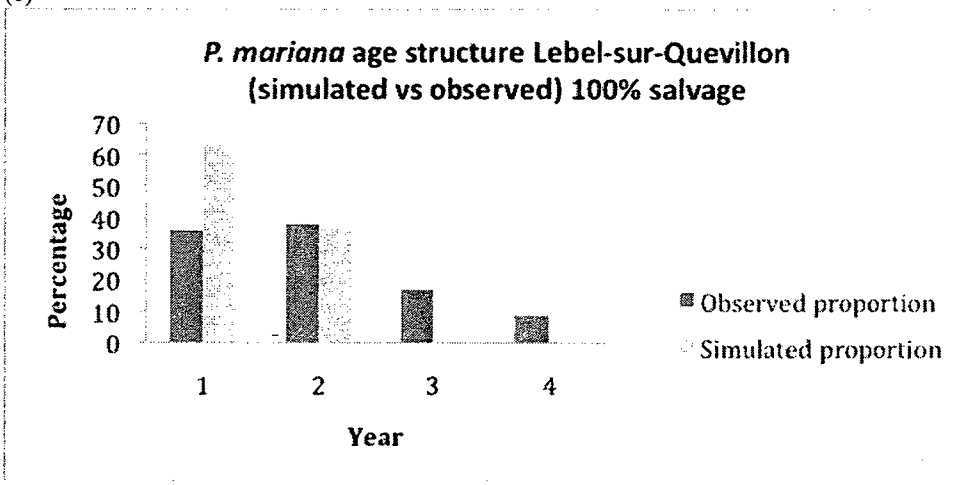
(a)



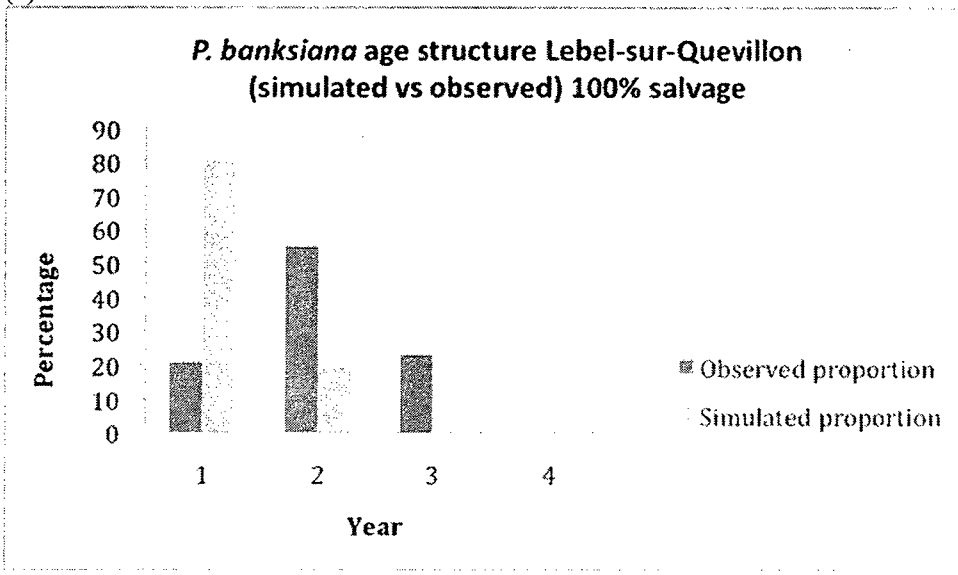
(b)



(c)



(d)



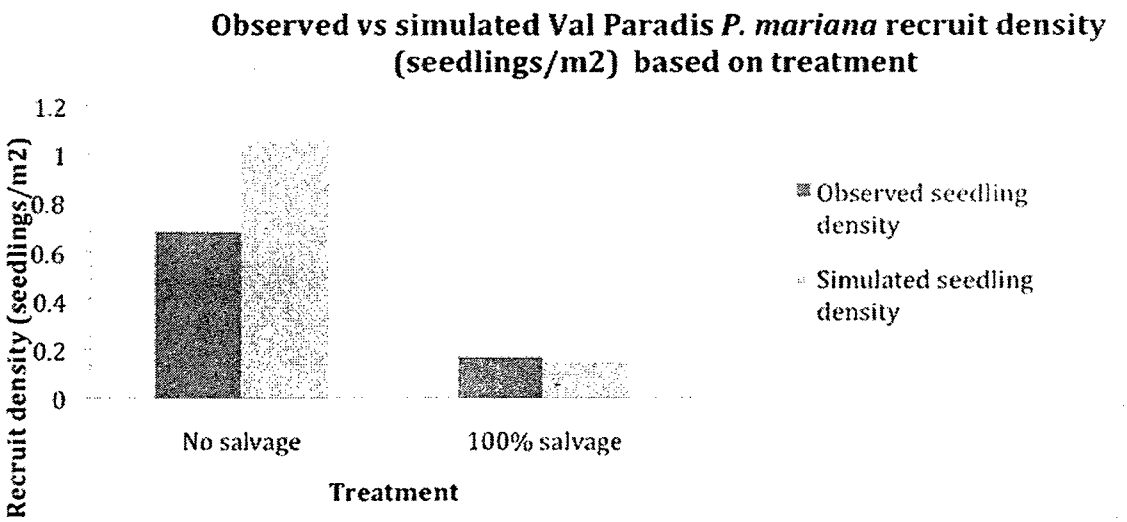
Observed seedling densities and age structures for *P. mariana* and *P. banksiana* (averaging across 36 stands) from the Val Paradis wildfire (Greene *et al.* (2006) and Greene *et al.* (2004)) were compared to model predictions. Salvage month for the Val Paradis wildfire for use in the simulations was set at 4 (In reality, salvage began in August and lasted until December; we chose October (the median month). The seedbed proportions in the unsalvaged stands for this mainly lowland site 315 km to the west of Lebel-sur-Quevillon, were astonishingly similar to those of Lebel-sur-Quevillon: mineral

soil and humus 1%, living *Sphagnum* and feathermoss 10%, high porosity duff 79%, and lethal 10%. The basal area per area for these mixed stands of *P. banksiana* and *P. mariana* averaged 0.002.

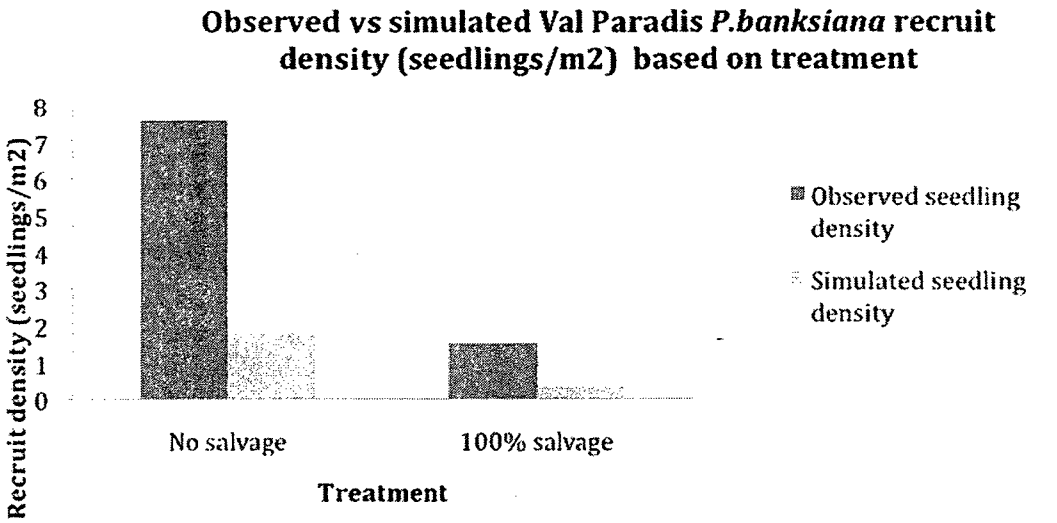
The model predicted a *P. mariana* regeneration density of 1.06 seedlings/m^2 for a burned unsalvaged stand and 0.15 seedlings/m^2 for a 100% salvaged stand. Observed regeneration densities were within 40% of predicted values: 0.68 seedlings/m^2 in the burned unsalvaged stands and 0.17 seedlings/m^2 in the 100% salvaged stands (Figure 6a).

For *P. banksiana* the model badly under-predicted the regeneration. It simulated a natural regeneration density of 1.78 seedlings/m^2 for the burned unsalvaged stands and 0.38 seedlings/m^2 for the 100% salvaged stands. Observed natural regeneration densities were 7.57 seedlings/m^2 and 1.51 seedlings/m^2, respectively (Figure 6b).

Figure 6. Observed vs simulated seedling densities at Val Paradis for *P.mariana* (a) and *P. banksiana* (b)
(a)



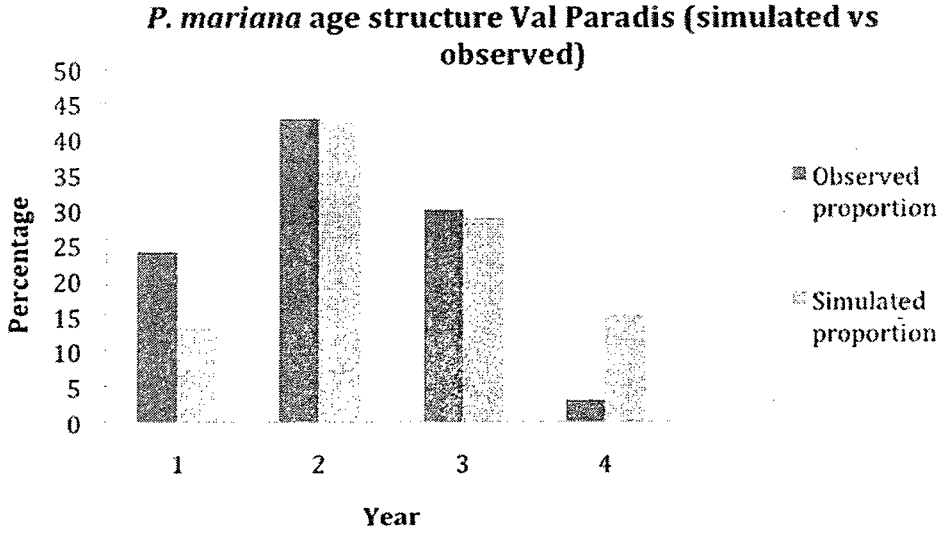
(b)



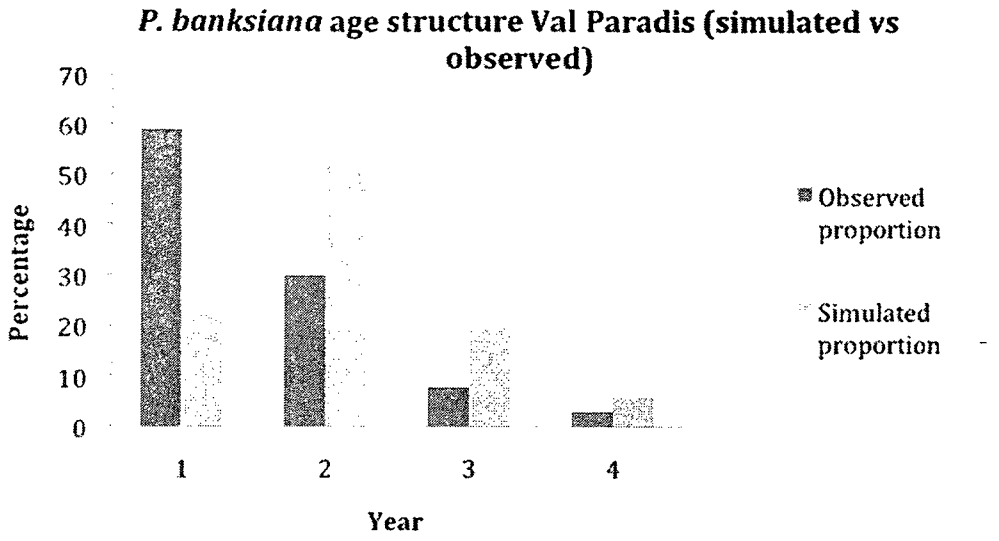
Simulated age structures for *P. mariana* (Figure 7a) in the non-salvaged stands at Val Paradis were concordant with the observed values. For *P. banksiana* (Figure 7b), the model badly underpredicted the size of the first summer cohort.

Figure 7. Val Paradis observed and predicted *P. mariana* (a) age structure and *P. banksiana* (b). Both are for a no salvage treatment.

(a)



(b)

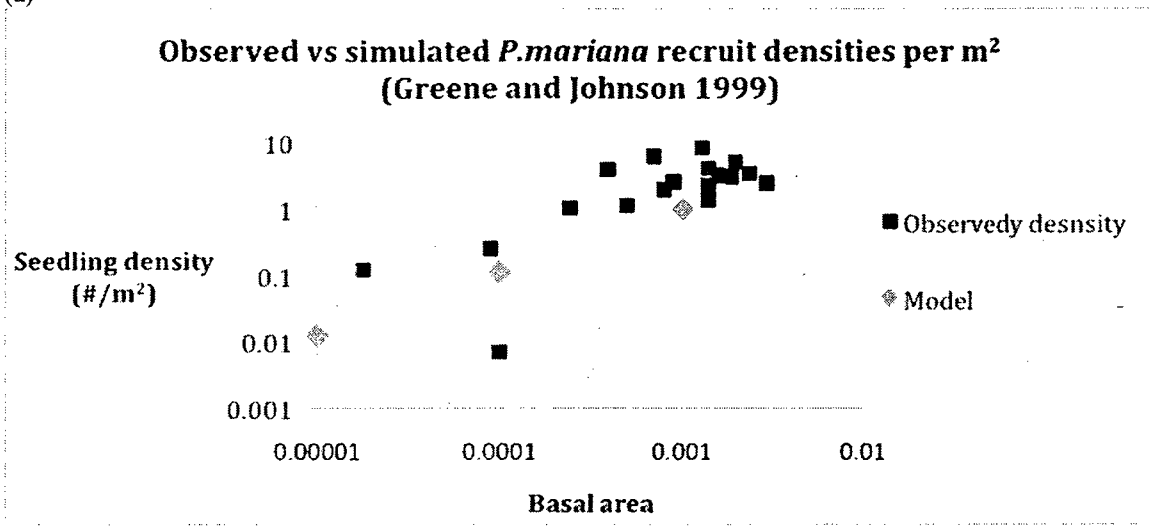


Greene and Johnson (1999) examined a 6-year-old wildfire on much drier sites than the two Quebec fires described thus far. None of the 18 *P. mariana* and 19 *P. banksiana* stands they examined had been salvaged; and they developed regressions for the two conifer species relating seedling density (recruits/m^2) to pre-fire basal area per area. While their observed seedbed proportions were quite different from the two Quebec fires: mineral soil and humus 17%, living *Sphagnum* and feathermoss 0%, thick duff 74%, lethal substrates 9%, nonetheless if we regard these proportions merely as being for good, poor, and lethal seedbeds, then they are similar to the Quebec fires.

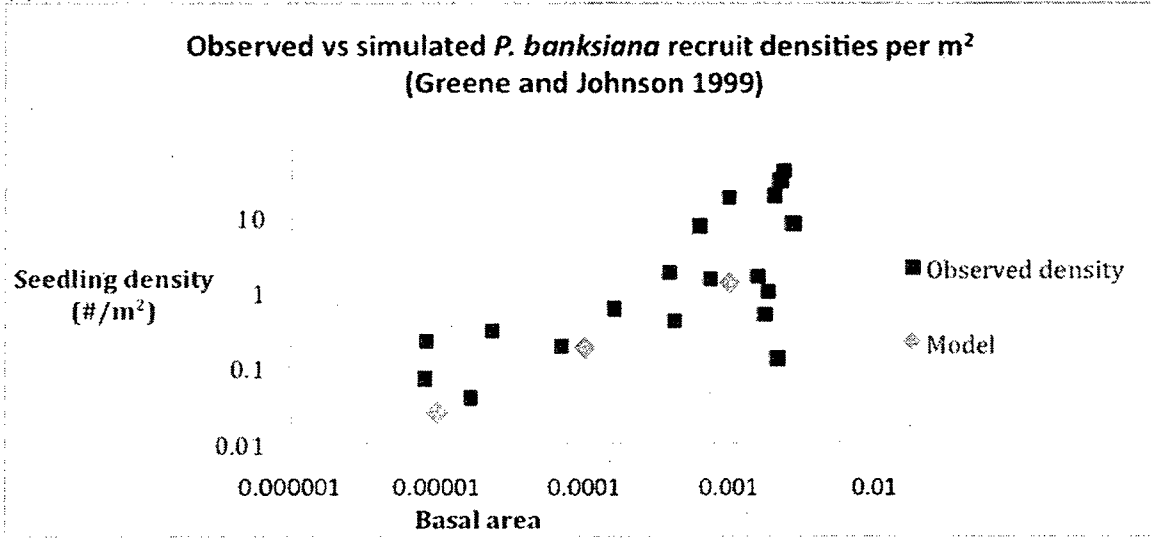
Simulated seedling densities at a range of basal area per area values for *P. mariana* (Figure 8a) and *P. banksiana* (Figure 8b) were compared to the regression lines of Greene and Johnson (1999). Across the range of basal area per area of 0.00001 to 0.002, the model underpredicted the recruitment density of *P. mariana* by, at most, 15%. The model overpredicted *P. banksiana* recruitment density by at most 30% across the same range.

Figure 8. Observed and simulated *P. mariana* (a) and *P. banksiana* ((b) seedling densities vs. basal area for a Saskatchewan fire.

(a)



(b)



Prescriptive simulations

The simulations indicated that, not surprisingly, delaying salvage increased the regeneration density because there were fewer seeds to be removed due to the on-going abscission. For *P. mariana* to minimally achieve full stocking with 100% salvage required a delay in harvesting until the fourth winter with basal area per area as low as 0.001 (Table 1). A delay until only the second winter permited full stocking with a

minimum basal area per area of 0.00175. First winter salvage did not provide full stocking at any reasonable (<0.003) value of basal area per area.

P. banksiana required less of a delay to achieve adequate stocking (Table 1). A basal area per area of only 0.001 could fully stock the site with a delay only the second winter. Full stocking with a first winter harvest could be achieved if the basal area per area was at least 0.0025.

Table 1. The year of 100% winter salvage in which minimally full stocking can be obtained given the pre-fire basal area/area

Basal area/area	*P. mariana*	*P. banksiana*
0.001	4	2
0.00125	3	2
0.0015	3	2
0.00175	2	2
0.002	2	2
0.00225	2	2
0.0025	2	1
0.00275	2	1
0.003	2	1

The second set of simulations looked at the additional factor of salvage intensity (Table 2). Of course, as the intensity of salvage decreased, the regeneration was augmented because fewer seeds were removed from the site and better seedbeds were available after the passage of the harvesters. For *P. banksiana*, full stocking could be achieved at any pre-fire basal area from 0.001 to 0.003 if the salvage was delayed until the second winter (Table 3). With first winter salvage, full stocking was possible if only 40% of the area was salvaged.

Table 2. The maximum percentage of a stand that can be salvaged for *P. mariana* to achieve 1 seedling/m^2 given a winter salvage date (first through third years) and the prefire basal area per area

Basal area/area	Year 1	Year 2	Year 3
0.001	0	0	60
0.00125	0	60	100
0.0015	52	85	100
0.00175	65	97	100
0.002	72	100	100
0.00225	78	100	100
0.0025	81	100	100
0.00275	84	100	100
0.003	87	100	100

Table 3. The maximum percentage of a stand that can be salvaged for *P. banksiana* to achieve 1 seedling/m^2 given a winter salvage date (first through third years) and the prefire basal area per area

Basal area/area	Year 1	Year 2	Year 3
0.001	40	100	100
0.00125	67	100	100
0.0015	79	100	100
0.00175	87	100	100
0.002	92	100	100
0.00225	96	100	100
0.0025	99	100	100
0.00275	100	100	100
0.003	100	100	100

The third and final simulations examined the effect of the redistribution of seeds (via a chipper) on final seedling density. The amelioration is more pronounced for *P. mariana* (Table 4; Table 5) because there were more seeds to redistribute due to its slower abscission schedule. For both species, any basal area per area value as low as 0.001 was sufficient to achieve adequate stocking, even with a first winter harvest.

Table 4. *P. mariana* seedling density vs basal area/area following 100% salvage and 75% re-dispersal of salvaged seeds in the first 3 winters following fire

Basal area/area	Year 1	Year 2	Year 3
0.001	1.72	1.47	1.34
0.00125	2.12	1.81	1.66
0.0015	2.52	2.16	1.97
0.00175	2.92	2.5	2.28
0.002	3.32	2.84	2.59
0.00225	3.71	3.17	2.89
0.0025	4.1	3.5	3.2
0.00275	4.49	3.84	3.5
0.003	4.87	4.17	3.8

Table 5. *P. banksiana* seedling density vs basal area/area following 100% salvage and 75% re-dispersal of salvaged seeds in the first 3 winters following fire

Basal area/area	Year 1	Year 2	Year 3
0.001	1.97	1.62	1.53
0.00125	2.38	1.96	1.85
0.0015	2.79	2.3	2.17
0.00175	3.18	2.62	2.48
0.002	3.57	2.94	2.78
0.00225	3.95	3.26	3.07
0.0025	4.32	3.56	3.36
0.00275	4.69	3.87	3.65
0.003	5.06	4.17	3.93

Discussion

Generally, the model performed adequately. As expected, both observed and simulated seedling densities declined as the proportion of the forest that was salvaged increased. The largest age classes we observed were in the first three years, as predicted. Nonetheless, a more detailed examination reveals that the model is problematic.

The density of *P. banksiana* at Val Paradis was badly underpredicted (four-fold) at both the non-salvaged and 100% salvaged stands. Likewise, density was underpredicted at the 100% salvage Lebel-sur-Quevillon stand by 4 times. Prediction of density was good only at the Saskatchewan fires where it was slightly over-predicting, but still within 30% or less of the (observed) regression values.

For the age class structure of *P. banksiana*, we greatly overestimated the relative contribution of first summer seedlings in the 100% salvage site at Lebel-sur-Quevillon, while badly underestimating the contribution of that same cohort in a non-salvage site at Val Paradis. This could be of course due merely to weather-related events in the first summer at either fire. As seen in Chapter 2, the abscission study for *P. banksiana* showed a large difference in first year abscission for the two fires examined there. More

worrisomely, at the Lebel site (100% salvage), 24% of the seedlings arise after the second summer, something the model says is impossible. This latter contribution is far too large to be due to long distance dispersal from unburned stands as we deliberate sampled stands far from any edge.

It seems likely to us that the underestimation of *P. banksiana* density at both salvaged and unsalvaged stands is due to either (1) the first year inhibiting effect of ash being weaker than we suppose for this species, and/or (2) the seedbed-mediated survivorship being better for this species than suggested by the model. As for the large fraction of seedlings arising in the third summer, although this will not be enough to explain a 4-fold underestimate of the density it will certainly help diminish the underprediction of total density.

Nonetheless, it is disturbing that the model cannot explain the presence of that extra cohort. As mentioned it cannot be long distance dispersal. Further, there is no empirical documentation of a long-lived seedbank on or within the soil surface for this species (or for *P. mariana*) (Johnson, 1975). The likely explanation is something that we failed to include the model simply because we had no data for it; namely, that many cone-bearing branches fall before the harvester reaches the stand or are knocked off the bole by the harvester. At such a low level above the ground, wind speeds will be far lower and thus the abscission rate will be much slower than entertained in the model.

As for *P. mariana*, overall density was predicted surprising well. At Lebel, the model was never in error by more than 50% (the partial salvage site); at Val Paradis, the model was within 35% of the correct amount; and at Saskatchewan the predicted

densities were always within 15% of the regression values based on the observed densities. Further, there was no pronounced tendency to under-predict or over-predict.

While the age structures were not as wildly incorrect as with *P. banksiana*, the 100% salvage site showed the same tendency for a large (25%) contribution from cohorts occurring after the second summer. Again, we assume this is due to cones lying at or near the surface that (1) were not removed off site as predicted by the model, and (2) abscised their seeds more slowly than expected.

With regard to the performance of the model, we conclude that this first attempt at a detailed expression of post-fire recruitment with and without salvage was generally successful, but clearly we require more data, especially for *P. banksiana*. The role of fallen branches could be examined easily enough by adding or removing cone-bearing branches at varying intervals after the second summer.

Turning now to the exploratory simulations, it was seen that *P. banksiana* is less harmed by early salvage than is *P. mariana*, a conclusion that tallies with observations made by Greene et al (2006). For example at Lebel-sur-Quevillon, for the 100% salvage stands, and with similar pre-fire basal area per area, the former had 10 times more seedlings per m^2 than the latter. The main reason is that much of the aerial seedbank of *P. mariana* still remains on the tree when early salvage occurs whereas it is expected that the *P. banksiana* cones will have few seeds left by that point.

While there are many commercially valid reasons to salvage early (St. Germain and Greene, 2009), according to the model one cannot obtain adequate regeneration of *P. mariana* unless salvage is delayed for until at least the second or third winter (depending on pre-fire basal area per area). *P. banksiana* can only be fully stocked after a first winter

salvage if the pre-fire basal area per area is very high. It would be useful to directly compare the cost of artificial regeneration vs the cost in lost or devalued wood given a delay. Further, delay would permit more of the fire-dependent insect taxa to successfully complete their life cycles, with consequent benefits for predators such as woodpeckers.

An alternative (or additional) to delay would be to harvest a fraction of the area. This should be done in parallel strips so that dispersal of seeds is not a constraint. Now, the good seedbeds created by the harvester would be available for a diminished but nonetheless on-site seed source. For example, for *P. mariana*, a basal area per area of 0.001 would confer full stocking only if the salvaged proportion were 0, while 50% salvage could be adequately stocked at a basal area per area of 0.0015. (Note that at our 50% salvage site at Lebel-sur-Quevillon we achieved only a seedling density of 0.23 seedlings/m^2, but the pre-fire basal area per area was only 0.001). For *P. banksiana*, even a small basal area per area (0.0012) would be sufficient with a first winter salvage operation if only 50% were salvaged. We point out that partial salvage, like delay, would be of benefit to those animal species dependent on recent fire.

Finally, the redistribution of seeds via a chipper is a promising method that would encourage high seedling densities of both species even when initial pre-fire basal area per area was low. Note however that our guess concerning the seed loss during passage through the chipper was unsupported by any empirical evidence and thus a field experiment is called for. Further, one would need to calculate the cost of the chipping operation relative to the cost of delay, partial salvage, and artificial regeneration.

In summary, our model is a promising method for exploring recruitment following wildfire. Introducing salvage permits the model to generate silvicultural

prescriptions. Indeed, the most obvious and quick utilization would be to couple the model with a pre-fire GIS-based inventory map so that for example sparse *P. mariana* stands would be salvaged after three years (or perhaps not at all), while more dense *P. mariana* and sparse *P. banksiana* stands would be salvaged at a shorter interval, and the most dense *P. banksiana* sites would be salvaged immediately. All the delays could be shortened insofar as the salvage became partial rather than complete.

Conclusion

The natural regeneration success of *Pinus mariana* and *Pinus banksiana* following fire is highly dependant on seed sources and the availability of suitable seedbeds. High intensity stand-replacing fires reduce organic layers by smoldering combustion, thereby increasing the proportion of favorable seedbeds, and meanwhile the flaming front opens the cones of these two serotinous species, thereby releasing stored seeds.

Post-fire duff layers that are thin or of lower porosity greatly enhance juvenile survivorship of sexually-recruiting boreal plant species. Nonetheless, there has been no study on duff compaction by snow following charring. In the first chapter we examined post-fire duff depth for the first 3 years (two winters) after a 2006 wildfire in the boreal forest of northwestern Quebec. We found that (1) significant compression was common, with (2) a positive relationship between the initial thickness of the burned organic layer depth and the subsequent amount of compression. The proportional compression rate was, however, roughly constant: about 14% after two years regardless of initial post-fire duff depth. We conclude that this amount of compression, given mean duff thickness immediately after fire, is too little to significantly impact post-fire seedling recruitment.

For aerial seedbank species, the seed abscission schedule following fire is of practical interest as it (1) affects the optimal timing of post-fire salvage operations that one might prescribe to maximize natural regeneration, and (2) is of theoretical interest as we would expect that the rapid decrease in age-specific survivorship on the better (thin duff) post-fire seedbeds due to leaf litter accumulation ought to select for rapid dissemination of seeds. Nonetheless, there are no published reports of the abscission

schedule of an aerial seedbank species from the fire date to several years after. In the second chapter, we found that (1) the schedules of a species were similar at both fires, and (2) the two species had very different rates of seed abscission with black spruce dispersing seeds from the cones at a significantly slower rate. Extrapolating from the regressions, we concluded that approximately 90% of jack pine and black spruce seeds will have been dispersed by 2 and 4 years, respectively, after a fire. Certainly, there are no reports of good post-fire seedbeds deteriorating so rapidly; the quick release we observe is evolutionarily advantageous.

In the third and final chapter we presented a model of the temporal dynamics of post-fire stand-level *Picea mariana* and *Pinus banksiana* natural recruitment response to salvage timing and proportion. The model incorporated: (1) seed availability as a function of basal area, salvage proportion and timing; (2) seed abscission as a function of time; (3) seedling survivorship as a function of seed mass, seedbed type frequencies, first summer ash, and granivory; (4) seedling and seed mortality as a function of salvage operations; and (5) re-dispersal of salvaged seeds via a chipper. Model simulations indicated that a delay in salvage, one to two years for jack pine and two to three years for black spruce, or a decrease in salvage proportion, can yield adequate natural regeneration densities. Further, either delay and/or partial salvage would also leave enough standing charred trees to satisfy the ecological needs of other species such as saproxylic beetles and woodpeckers. Further, this recommended approach would allow a company to avoid a costly investment in artificial regeneration. Further research is needed to determine the effectiveness of using a wood-chipper to re-distribute seeds following salvage as this empirical evidence is currently unavailable.

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